XIII. *On the Mechanism of the Male Genital Tube in* Coleoptera. By Frederick Muir.

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Plate XXI.

Although we have considerable knowledge of the skeleton of the male genital tube of a number of species of Coleoptera, but little is known as to the mechanism and muscles of this organ. Some of the most detailed work on this subject, such as Straus-Durckheim on *Melolontha vulgaris*, was done by workers who did not recognise the importance of the internal sac and the predominant rôle it plays in copulation. For these reasons the following remarks on some of the types and their manner of functioning, with a few details relating to muscles in a couple of " ring " types, may be of interest, notwithstanding their desultory character.

Orientation.

For the sake of clearness it is necessary to define the terms of orientation employed. For this purpose I accept for orientation the point between the abdomen and thorax, as defined by Dr. Sharp,* as basal. The portion of any segment or appendage nearest to that point being the base, and the portion most distant being the apex. In measuring the respective distances a continuous line on the body wall must be followed, a dorsal, pleural or ventral line for their respective areas. Thus the tarsus of a front leg lying against the basal point would still be the apex of the leg, and the coxa the base. This orientation applies equally to invaginations, struts or glands, and evaginations, tegminal lobes, etc. Thus the base of a tegminal lobe is that part nearest the body of the tegmen, and the apex is the free end; and the base of the tegminal strut is where it joins the tegmen, and the apex is the free end; the apex of the median lobe is the free end, and the base of the internal sac is where it joins the median lobe. The terms anterior or cephalic and posterior or caudal are relative to the head and tail, hence the anterior margin of a thoracic segment

* " Cambridge Natural History," V, " Insects," I, p. 112, fig. 62.

is the apical margin, and the anterior margin of an abdominal segment the basal margin. It is, however, not a good principle to use the terms anterior or posterior when discussing parts of an appendage.

The term invagination is applied to any withdrawal of the ectodermal surface into the body lumen, whether it be long and narrow, as is the case with the median struts in many beetles, or broad and short, as is the case with a large portion of the basal piece in many beetles.

Relation of Structure and Function.

A study of the skeleton, that is, of the membrane and the external and internal chitinisations of the male genital tube of Coleoptera, shows that there are several distinct types which it is reasonable to expect function in different ways, though little is known as to the method by which the sperm is conveyed from the testes to the spermatheca. One of the most interesting and instructive works on this subject is by Blunck on *Dytiscus marginalis.** He shows the formation of a spermatophore within the median lobe and the subsequent transference of the sperm to the female through a hole in the wall of the spermatophore. The median lobe of the Dytiscidae is funnel-shape, and there is no specialised internal sac; the Haliplidae and Pelobiidae are built on a similar plan, and there is good reason to believe that they form spermatophores in a similar manner to *Dytiscus.* The median lobe of the Gyrinidae is not funnel-shape, and it is highly probable that they do not form spermatophores, or if they do they are of a different shape to that of *Dytiscus.* These three families belong to the minor section of the Coleoptera, which has no specialised sac, whereas the major section has a large, more or less highly specialised sac, which is the chief organ of copulation. The shape of the sac and the armature upon it is often highly complex, especially the armature, called the transfer apparatus, round the functional orifice, where the ejaculatory duct opens on the internal sac. In some species this transfer apparatus takes the shape of a fine, long tube or flagellum. This is the case with the little Cucujid *Cryptomorpha desjardinsi*, which has a long sac and a long, slender flagellum; during copulation the long sac is entirely everted and enters the long membranous vagina, and the

* Zs. wiss. Zool. Leipzig, Bd. cii, Heft 2, pp. 169–248 (1912); also Carl Demandt, t.c. Bd. ciii, pp. 171–299 (1912) for the muscles.

long flagellum enters the long, spiral duct of the spermatheca. In this manner a complete tube is formed from the testes to the spermatheca. In *Anomala orientalis* the sac is large and the functional orifice is large and without any transfer apparatus; it is not brought against the opening of the duct of the spermatheca but to the opening of the bursa copulatrix, into which the sperm is discharged. By what means it is conveyed to the spermatheca it is impossible to say at present.

The coadaptation of the organs of the two sexes in a number of forms examined by Dr. Sharp and the writer is quite remarkable. A good case of this is in *Neolamprima adolphinae*, where the median lobe is small and produced into a very slender and long flagellum *; in the female the base of the duct leading to the spermatheca is widened and shaped like the median lobe; the more distal portion of the duct is very slender and spiral.

The fact that some Coleoptera are known to make spermatophores and the probability that others do not, suggests the possible division of the order into two groups. Whether this classification would separate certain families, or whether it would cut across several families separately it is impossible to say with our present knowledge. It is highly probable that when no specialised sac is present, especially if the median orifice be large, spermatophores are formed; when a sac is present and no specialised transfer apparatus exists it is possible, or even probable, that spermatophores are formed; but when a highly specialised transfer apparatus, especially if it be a flagellum, exists it is highly probable that no spermatophores are formed.

In the vast majority of Coleoptera the internal sac is the chief organ of copulation, the tegmen and median lobe acting as protectors and guides. In the following section the muscles explain the protrusion and retraction of the median lobe and tegmen and the retraction of the sac, but they do not explain the evagination of the sac. This is always brought about by blood pressure, and it is highly probable that the different types have followed certain lines of evolution to accommodate the different development of the sacs, and allow for their functional mechanism.

* This is not shown in Sharp and Muir, Trans. Ent. Soc. Lond., 1912, Pl. XLIV, figs. 10, 10*a*, as the authors failed to detect it at that time. As it is permanently everted it is easily broken during dissection.

It is among the trilobe forms of aedeagus that the sac is least developed; in many cases it cannot be distinguished from the ejaculatory duct, and in others it is only differentiated by a slight increase in size. In these cases it lies entirely within the median lobe. With the enlargement of the sac modifications have taken place in the median lobe and tegmen. These modifications have been mainly along three lines. The development of the median lobe into a bulb with the reduction of the tegmen (the Staphylinid type): the development of the median lobe into a long tube (the Phytophagoidea type): and the development of the tegmen into a more or less tubular organ (the Melolonthid type).

Something like the beginning of the Staphylinid type can be seen among the trilobe forms in *Syndesus cornutus*,* but it is among the Staphylinidae that this type reaches its most complete development. In that family such forms as *Gyrophaena pulchella* and *Zirophorus bicornis* have the median lobe cylindrical and the internal sac small, but in the latter the basal portion is slightly swollen and the dorsal surface but slightly chitinised, and it can be pressed down against the ventral portion; the median foramen is also very small. The line of development is for the apical portion of the median lobe to shorten and the basal portion to become enlarged and rounded, the ventral and dorsal areas to become chitinised, especially the former, with a band of membrane separating them. The dorsal surface can be brought towards the ventral surface by muscular contraction. Thus a complete automatous bulb is formed, which reaches a high state of perfection in such a form as *Xantholinus glabratus*. In many Staphylinidae if the aedeagus be dissected out of a freshly killed specimen and slight pressure be placed upon the bulb the sac will instantly be evaginated. The invagination of the sac is done by the contraction of muscles between certain areas on the sac and others on the median lobe. But there are innumerable stages between these forms among the Staphylinidae. This line of evolution has been followed in other groups such as Pselaphidae and some Malacoderms (i. e. *Telephorus limbatus* and *Balanophorus mastersi*).

* For figures and descriptions of the forms mentioned the reader is referred to Trans. Ent. Soc. Lond., 1912, pp. 477–642 and Plates XLII–LXXVIII.

The second line of development, the elongation of the tubular median lobe (the Phytophagoidea type), necessitates a greater or lesser amount of play between the median lobe and the tegmen. The limit to the length of a stiff, chitinous median lobe is soon reached on account of its want of flexibility, but this is overcome by a portion becoming membranous and thus capable of folding up. When the sac is shorter, or but little longer, than the median lobe the retractor muscles can ply between the sac and the median lobe, but when the sac becomes much longer than the median lobe this method of invagination would lead to a great crumpling up of the sac. This problem is met by one or two areas on the median lobe, to which the retractor muscles actuating the sac are attached, becoming invaginated, lengthened and chitinised. In this method the median struts arise which reach a wonderful state of perfection and slenderness in some of the Rhynchophora ; in the Longicorns the struts are long, wide and flat (a state also found in the Brenthidae). In this type the tegmen is reduced to a more or less slender ring and a strut, or even to a Y ; the tegminal lobes are found in every condition from large (Longicorns, Brenthids) to total absence.

The third type (the Melolonthid) is not so uniform as the other two, but equally worthy of notice. In this type the median lobe is greatly reduced and the tegmen is formed into a more or less complete tube. It is found in the Scarabaeidae and in certain Tenebrionidae. Every degree in size of the sac is found among these forms.

In the Staphylinid type, as we have already stated, there is an automatous bulb with a small foramen, which by contraction can exert blood pressure upon the sac. In the Phytophagoidea and Melolonthid types there is no such development of the median lobe, and the median orifice is large. The blood pressure must therefore be brought about by some other mechanism. In the Phytophagoidea type, and in many of the Melolonthids, this is most likely effected by the reduction of the abdominal cavity, either by the contraction of the abdominal walls or by the distention of the air sacs in the abdomen, or by a combination of the two.

In *Melolontha vulgaris* Straus-Durckheim describes and figures some large muscles, which he styles " les deux chefs du constricteur du canal ejaculatoire." In an *Anomala* which I have examined these form a large bulb of circular muscles at the base of the median lobe, the basal edge being connected to the base of the median lobe. These muscles do not touch the ejaculatory duct or the sac except where the former passes through from the body cavity. When retracted the apex of the sac and a length of slack ejaculatory duct lie loose within this muscular bulb. That these muscles do not act as constrictors of the duct or sac is perfectly evident, and it is very highly probable that they act as a bulb for the evagination of the sac. The retractors of the sac are shown in Straus-Durckheim's work arising from different parts of the sac and proceeding to a point apparently on the wall of the muscular bulb. It would at first appear as if these retractor muscles had no connection with the median lobe, but this is not the case, for the dorsal strut of the median lobe proceeds as a membrane to this point and the muscles are attached to its apex. *Geotrupes sylvaticus* has a very small unspecialised sac, a very small median strut and no muscular bulb, and is a very much simpler structure.

Dr. Sharp called my attention to some peculiarities of the sac of *Anoplognathus*. Upon examination I find that there are three ducts opening on the sac at three distinct spots. Two of these are of a similar nature and the third apparently of a glandular nature; there is also a short diverticulum which also appears to be of a glandular nature. Whether the two similar ducts proceed separately to the testes I am unable to say from examining only dried specimens. There is also a strange arrangement of the female uterus.

Musculature.

As two representatives of the Phytophagoidea type I have selected *Rhynchophorus ferrugineus* and *Strangalia armata*. The *Sphenophori* differ from the other Rhynchophora in possessing a pseudotegmen formed by the chitinisation of part of the membrane connecting the tegmen with the body wall, and by the eighth abdominal segment being invaginated within the seventh, the pygidium being formed by the seventh tergite. In *Strangalia armata* not only are the eighth tergite and sternite well developed, but there is a well-developed ninth segment, a condition not found in any of the Rhynchophora. I do not know if this distinction holds throughout the Longicornia, but should it do so it will be of great importance.

Figure 1 represents in a semidiagrammatic manner the skeleton of the male genitalia of *Rhynchophorus ferrugineus*. The seventh tergite is large and forms the pygidium, its apical margin meets the apical margin of the seventh sternite and closes the outer cloaca. The eighth tergite is much smaller and fits into the convexity of the ventral side of the seventh tergite, to which it is connected by a large membrane allowing of considerable play. The basal margin of the eighth tergite is produced into two large, flat processes or struts to which the protractor muscles are attached and allow of greater play. The eighth sternite is small and together with the eighth tergite closes the inner cloaca. The apical margins of the eighth segment is connected to the base of the tegmen by a large membrane (*im 1* and *ptg*), the median portion of which is chitinised and forms the pseudotegmen. At the base where it joins the eighth segment this membrane forms a narrow tube (shown too large in the figure), which allows of the median lobe moving through it but does not admit of any lateral motion. The anus (*an*) opens on the membrane beneath the eighth tergite. The tegmen consists of a strong chitinous ring (*tr*), incomplete on the dorsal area where the chitin curves slightly apically but does not meet, and a large, strong strut (*tgs*) which varies somewhat in shape and size in different specimens, the one figured (1 *a*) being large and broad at the apex; a strong keel runs down the dorsal surface of the strut. The median layer or median tube consists of the median lobe and the membrane connecting it to the tegmen. The median lobe is a tube incompletely chitinised, the ventral plate being nearly divided into three pieces by two deep, narrow membranous areas; the basal corners of the ventral plate are continued as two narrow struts (*ms*); the dorsal plate is produced basad farther than the ventral plate. The median struts (*ms*) at first form chitinisations on the surface of the median lobe and later join the invaginations which form the free struts. The internal sac (*is*) lies within the median lobe.

The chief muscles which control the movements of this skeleton are (fig. 2) :—

(*a*) Retractor and protractor muscles from the pseudotegmen to the eighth segment, by which the pseudotegmen is held firmly in its place and moved through a limited distance.

(*b*) A large series of muscles from the apex of the pseudotegmen to the large apical portion of the tegminal strut (*tgs*). This holds the ring of the tegmen into the base of the pseudotegmen, where it fits quite tightly, the membrane connecting the pseudotegmen and the tegmen forming a fold between them.

(*c*) The retractor of the median lobe connects the base of the median lobe and the base of the median struts with the inner surface of the apex and the ridge of the tegminal strut.

(*d*) The protractor of the median lobe connects the ring of the tegmen (*tr*) with the outer surface of the apex of the median struts.

(*e*) The retractors of the internal sac connect certain points (e^1, e^2, e^3, figs. 3, 4) on the sac with the inner surface of the apex of the median struts. At the point on the sac where the largest of these muscles (e^3) is attached there is a large Y-shaped sclerite. A few small muscles connect the basal portion of the sac (*g*) with the median lobe near its apex. When it is remembered that the median struts are invaginations or prolonged folds of the median lobe it will be seen that all the muscles of the internal sac are in fact attached to the median lobe.

Figure 5 represents in a semidiagrammatic manner the skeleton of *Strangalia armata* with the internal sac partly evaginated. In this species of Longicorn the eighth tergite is well developed and forms the last visible segment; the eighth sternite (fig. 7, VIII) is small and membranous with two small triangular chitin plates and a short strut or spiculum. The ninth tergite (fig. 6, 9) is distinct and forms a small arc, each corner of which is produced into a small spiculum (*lsp*); the ninth sternite (IX) is well developed and produced into a large spiculum (*sp*). The membrane (*im 1*) connects the ninth segment with the tegmen. The tegmen consists of a "ring" with a pair of large, dorsal-tegminal lobes (fig. 5, *tgl*), the ventral portion being produced into a large strut (*tgs*), the chitinisation not meeting till the apex. The median lobe is tubular with a gusset of membrane along each lateral area, the ventral chitinisation extending further distad than the dorsal and is pointed and hooked at the apex, the base is produced into two wide struts (*ms*). The base of the struts and the base of the body of the lobe is indicated by the attachment of the membrane (*im 2*) which connects the tegmen with the median lobe. The internal sac is very long, simple, cylindrical, bent about half-way and again near the apex, with two small subcrescent-shaped sclerites near the base and a semichitinised patch near the apex; there is no complex transfer apparatus.

Muscles connect the spiculum of the eighth sternite with the seventh sternite (fig. 7), and a larger series of muscles connect the plates of the eighth sternite with the large spiculum of the ninth sternite. These muscles hold the ninth sternite and its spiculum in place and take off the strain of the protractors and retractors of the tegmen (*g* and *b*). A few bundles of muscle connect the small spiculum of the ninth segment to the connecting membrane, and others connect it with the walls of the rectum (fig. 6, *m*, *k*, *l*).

The retractor of the tegmen (figs. 7, 8 *b*) consists of a large series of muscles attached to the membrane (*im 1*), mainly on its right side and near its junction with the tegmen, and to the apex of the spiculum (*sp*).

The protractor of the tegmen (*g*) consists of a large bundle of muscles from the inner surface of the base of the spiculum of the ninth sternite to the apex of the tegminal strut.

The retractor of the median lobe consists of a long muscle from the inner surface of the apical half of the median lobe to the apex of the tegminal strut (fig. 8 *c*).

The protractor of the median lobe (fig. 8 *d*) proceeds from the ring of the tegmen to the apical portion of the median struts.

Retractors of the internal sac (fig. 8 *e*) are very long and fine muscles from the apex of the median struts to areas on the internal sac, a few to the crescent-shaped sclerite near the base of the sac, and others to the semichitinous area near the apex. There are other small bundles from the sac to the inner surface of the median lobe.

Another muscle (fig. 8 *n*) connects the apex of the tegminal strut with the apex of the median struts. This would help to co-ordinate the movements.

To those who are interested in the mechanism of insect-structure these few notes may be of interest, and may lead them to work on the details of various forms. The task is huge, and the information desired is harder to procure than that relating to the external morphology, but no final "natural classification" can be attained without studying the male genitalia, and the mechanism and function are an important part of that study.

My thanks are due to Dr. David Sharp, who has been at work on these structures for several years and has accumulated a mass of material and information, both of which have been freely placed at my disposal. The material used for *Rhynchophorus* was supplied to him by Prof. Bainbrigge Fletcher of Pusa.

Explanation of Plate XXI.

Figures 1–4 are of Rhynchophora; 5–8 of *Strangalia* (Longicornia).

Fig. 1. Lateral view of skeleton of the male genitalia of *Rhynchophorus ferrugineus*.

1*a*. Tegminal strut.

2. Lateral view of pseudotegmen and muscles of aedeagus.

3. Apex of internal sac showing the attachment of muscles.

4. Internal sac evaginated.

5. Lateral view of skeleton of the aedeagus of *Strangalia armata*, with internal sac partly evaginated.

6. Ventral view of ninth abdominal segment of *S. armata*.

7. Eighth and ninth sternites of *S. armata*, with muscles attached.

8. As fig. 5, but with the muscles.

an. Anus.
ej. Ejaculatory duct.
fo. Functional orifice.
im 1. Membrane between tegmen and body wall.
im 2. Membrane between tegmen and median lobe.
lsp. Lesser spiculum.
ml. Median lobe.
mo. Median orifice.
ms. Struts of median lobe.
ptg. Pseudotegmen.
sp. Spiculum.
tgs. Tegminal strut.
tr. Tegminal ring.
8. Eighth tergite.
9. Ninth tergite.
VIII. Eighth sternite.
IX. Ninth sternite.
a. Retractor and protractor muscles of pseudotegmen.

b. Muscles between the apical edge of pseudotegmen and apex of the tegminal strut (fig. 2). Retractor of tegmen (figs. 7, 8).

c. Retractor of the median lobe.

d. Protractor of the median lobe.

e. Retractor of the internal sac.

e^1, e^2, e^3. Areas to which retractor muscles of internal sac are attached.

f. Apical edge of pseudotegmen.

g. Sclerite at base of the internal sac (fig. 4). Protractor of tegmen (figs. 7, 8).

k. Muscles from the lesser spiculum to the walls of rectum.

l. Muscles from lesser spiculum to the walls of rectum.

m. Muscles from lesser spiculum to connecting membrane *im 1*.

n. Muscles from apex of tegminal strut to apex of median struts.